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BIOLOGICAL OBSERVATIONS ON THREE *TRYPOXYLON* WASPS IN THE SUBGENUS *TRYPARGILUM*[1] FROM COSTA RICA: *T. NITIDUM SCHULTHESSI, T. SAUSSUREI,* AND *T. LACTITARSE* (HYMENOPTERA: SPHECIDAE)

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The genus *Trypoxylon* subgenus *Trypargilum* occur in temperate and tropical regions of the Western Hemisphere (Bohart and Menke, 1976). These solitary spider wasps are either mud daubers or they nest in pre-existing cavities. They are unusual among all wasps in that males normally remain in nests as guards while females forage (Peckham and Peckham, 1895; Rau, 1928; Fattig, 1936; Paetzel, 1973; Coville and Coville, 1980). In addition, many species groups and complexes of *Trypargilum* appear to have distinctive nest architecture, cocoon morphology, and prey preferences (Krombein, 1967; Matthews and Matthews, 1968; Lin, 1969; Coville, 1979). The last three traits may become useful taxonomic characters when information becomes available on more species, especially in the Neotropics. Coville and Coville (1980) recently reported on the biology of *Trypoxylon* (*Trypargilum*) *tenoctitlan* Richards in Costa Rica. The purpose of this paper is to present biological data obtained from nests of three other Costa Rican *Trypargilum* during that study: *T. nitidum schulthessi* Richards, *T. lactitarse* Saussure, and *T. saussurei* Rohwer.

Methods

Trap-nests with borings of 4.8, 6.4, and 9.5 mm drilled to a depth of 152 mm were used to obtain wasp nests. Coville (1979) and Coville and Coville (1980) describe the technique in detail.

The study was conducted in 1975 in Guanacaste Province, Costa Rica. One study site was 25 km SW of Bagaces at the Organization for Tropical Studies Field Station at Palo Verde on the Comelco Property. Two other sites were 4 km NW Cañas at La Pacifica 1) in the riverine forest along the Rio Corobici and 2) on the porch of a cabin.

Trypoxylon (*Trypargilum*) *nitidum schulthessi* Richards

Richards (1934) placed *T. nitidum* Smith in the subgroup of *T. nitidum* (=*nitidum* complex) of the *nitidum* group. This polytypic species is found

[1] The author prefers to treat *Trypargilum* as a subgenus until its relationship to the diverse species groups of subgenus *Trypoxylon* is carefully studied.

Table 1. Contents of 6 *Trypoxylon nitidum schulthessi* nests from La Pacifica, Costa Rica.

	Rio Corobici		Cabin Porch
	Bore Diameter (mm)		
	6.4	4.8	4.8
Nests examined	1	2	3
Provisioned cells	8	7	22
Cells provisioned but without wasp egg	1	–	1
Cells with contents preserved or died	–	3	7
Wasps Reared:			
T. nitidum schulthessi ♂♂	–	1	6
♀♀	3	3	9
Natural Enemies Reared:			
Chrysididae			
Neochrysis lecointei (Ducke)	4	–	–
Acarina			
Pyemotes sp.	–	–	1

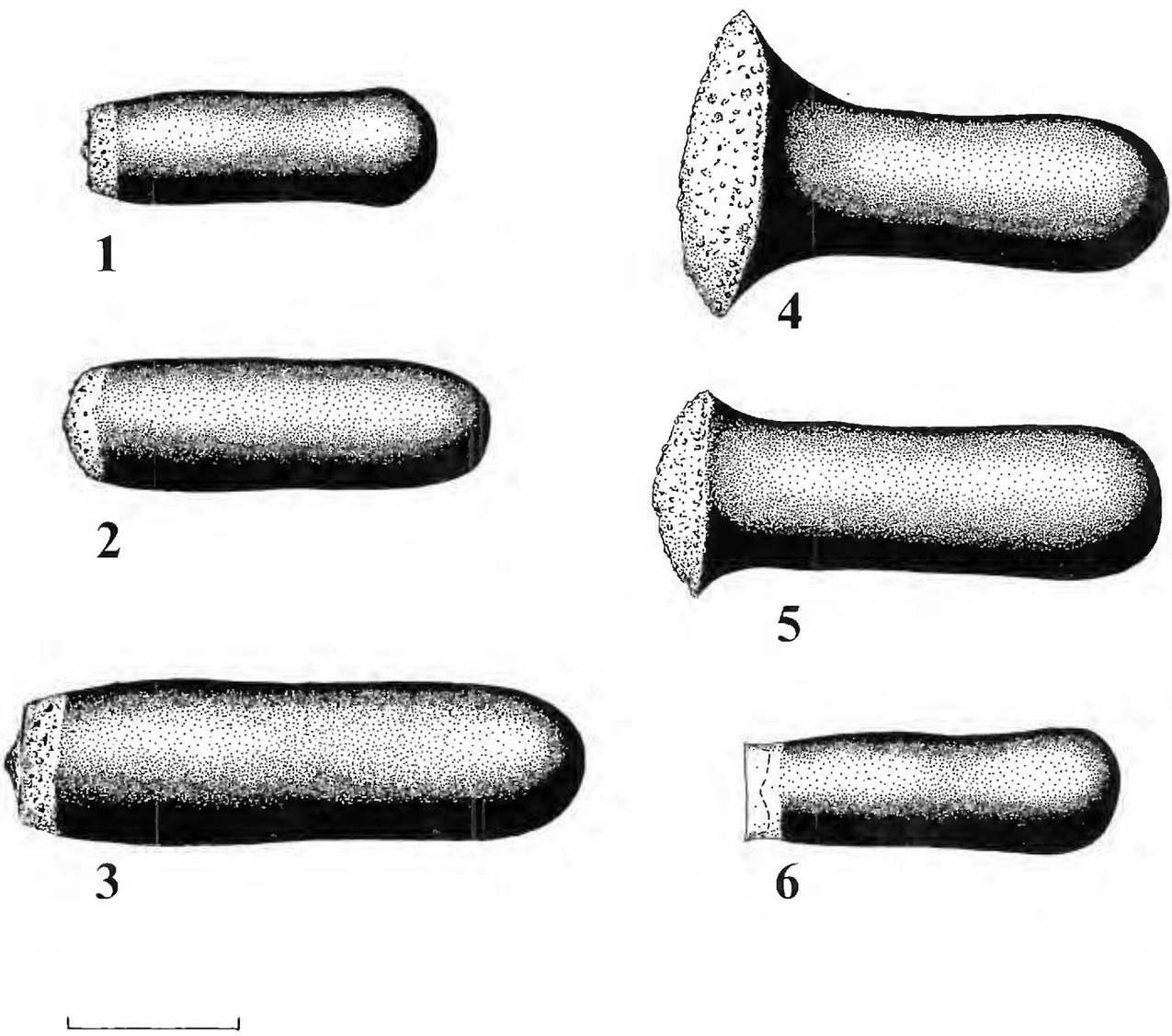
throughout the tropics. *Trypoxylon nitidum schulthessi,* previously known only from the original description of Richards (1936), occurs in Costa Rica.

This species occupied 6 trap-nests at La Pacifica, Costa Rica. Three traps were from one bundle set out in the narrow forest along the Rio Corobici. The other three were from bundles attached to a chair on the cabin porch. One nest from the Rio Corobici was in a 6.4 mm boring; the other 5 were in 4.8 mm borings. Contents of these nests are summarized in Table 1.

Adult behavior.—On February 7, each of two pairs of *T. nitidum schulthessi* entered trap-nests on the cabin porch. The males followed the females that were searching for nests. Thereafter, the males remained in the nests as guards with their heads facing outwards at the nest entrance. Three marked males and two marked females of *T. tenoctitlan,* a larger species, were observed trying to enter the nests of *T. nitidum schulthessi.* The guard (presumably the male) successfully defended his nest except for one extremely aggressive female that had to be repeatedly driven away (see Coville and Coville, 1980).

One of the wasps in each of the nests on the porch regularly spent the night away from the nest and returned at 0647–0732 AM CST, a time which was 7–29 minutes before the males of *T. tenoctitlan* returned to their nests. At that time air temperature was about 25°C.

When the female returned to the nest with prey, she alighted at the entrance. The male guard then left the tunnel, mounted the female's back, and attempted to copulate as the female entered the nest head first.



Figs. 1–6. Cocoons of *Trypargilum* (anterior on the left). Fig. 1. *T. nitidum schulthessi*. Fig. 2. *T. tridentatum*. Fig. 3. *T. orizabense*. Fig. 4. *T. tenoctitlan* from trap-nest with 9.5 mm diameter tube. Fig. 5. Same from 6.4 mm trap-nest. Fig. 6. *T. clavatum*. Scale equals 5 mm.

One of the 2 nests started on February 7 was completed on February 16 and contained 8 provisioned cells; the other nest was completed on February 18 and contained 6 provisioned cells.

Nest architecture.—Nests consisted of a linear series of provisioned cells separated by mud partitions, followed by one or more vestibular cells, and a mud closure plug. A preliminary mud plug was always present at or near the inner end of the trap-nest boring. The 6.4 mm nest contained 8 provisioned cells and one vestibular cell. The 4.8 mm nests contained 2 to 8 provisioned cells and 2 or 3 vestibular cells. Closing plugs consisted of 2 elements resembling 2 thickened, closely spaced cell partitions. Closing plugs were at the entrance in 4 nests but were recessed 12 mm in the 6.4 mm nest and 18 mm in one of the 4.8 mm nests. The last nest contained only 2 provisioned cells. Nest dimensions are shown in Table 2.

Prey.—Cells were provisioned with 7 to 17 spiders ($\bar{x}$ = 10.9, N = 7). Identifications of 52 spider prey are as follows:

ARANEIDAE: 2 ♂♂ *Eustala* sp.; 4 imm., 2 ♀♀, 5 ♂♂ *Metazygia* sp.; 2 ♂♂ *Metepeira* sp.; 34 imm. undetermined Araneidae.
THERIDIIDAE: 3 ♀♀ *Theridion* sp.

Life history.—The egg, about 2 mm long, is attached to the abdomen of one of the last spiders stored. Eclosion of the larva takes place about 1–1.5 days after the egg is laid. One larva completed feeding on 12 spider prey in about 2 days, spent 2 days spinning its cocoon, and then pupated 7 days later. The imaginal molt occurred after 20 days, but the adult waited 4 more days before attempting to chew through the gelatin capsule in which it was confined for observation.

The time interval from nest completion to emergence of the adult from the cocoon is 34 to 49 days. No diapause or quiescent stage was noted. The distribution of the sexes in the nest appears to be random.

The cocoon is dark brown, varnished in appearance, and brittle. It is cylindrical with the posterior end rounded; the anterior end is truncate with a median nipple, which is gray and more coarsely granular than the rest of the cocoon (Fig. 1). Two male cocoons were 8.7 and 9.5 mm long and 2.9 mm wide. Six female cocoons ranged 9.7–11.0 mm long ($\bar{x}$ = 10.2) and 3.0–3.6 mm wide ($\bar{x}$ = 3.3).

Natural enemies.—Four females of *Neochrysis lecointei* (Ducke) were reared from the 6.4 mm nest (Table 1). The chrysidids emerged from March 25 to 31, whereas 3 females of *T. nitidum schulthessi* reared from the same nest emerged on March 15 and 16. This late emergence of the parasite is unusual [and perhaps indicates poor adaptation of *N. lecointei* to *T. nitidum schulthessi.*] The innermost cell in one of the 4.8 mm borings was infested by *Pyemotes* mites.

Trypoxylon (*Trypargilum*) *lactitarse* Saussure

This species occurs from Canada to Argentina. Richards (1934) placed *T. lactitarse* (under the name *cinereum*) in the *punctulatum* group. Its biology (under the names *striatum* and *albopilosum*) is well known in North America (Peckham and Peckham, 1895; Rau, 1928; Krombein, 1967; Medler, 1967).

Trypoxylon lactitarse occupied 2 trap-nests in Costa Rica. A 9.5 mm nest was from a bundle set out on January 12 at the Rio Corobici site at La Pacifica. The nest was collected on January 31 along with the female wasp that was constructing the closing plug. No male wasp was observed at the nest. A 6.4 mm nest set out on January 14 at Palo Verde was collected on February 25 and had a chrysidid emergence hole in the closing plug.

Nest architecture.—Nest structure was similar to that of *T. nitidum schulthessi.* Both *lactitarse* nests had preliminary mud plugs deposited at the inner end of the tunnels. The 9.5 mm nest had 7 provisioned cells and 1

Table 2. Nest dimensions of *Trypoxylon* subgenus *Trypargilum* from trap-nests in Costa Rica.

Species	Nest Diameter (mm)	Sex	Provisioned Cell Length (mm) Mean	SD	(N)	Vestibular Cell Length (mm) Mean	SD	(N)	Cell Partition Thickness (mm) Mean	SD	(N)	Closure Plug Thickness (mm) Mean	SD	(N)
nitidum schulthessi	6.4	♀	12.4 ± 1.4		(5)	31.7		(1)	0.5 ± 0.1		(8)	1.4		(1)
		♂	—											
	4.8	♀	13.7 ± 1.8[1]		(8)	26.4 ± 31.5		(9)	0.6 ± 0.2		(22)	2.7 ± 1.3		(4)
		♂	11.1 ± 1.5		(7)									
lactitarse	9.5	♀	18.6 ± 0.1		(2)	11.0		(1)	1.2 ± 0.2		(7)	—		
		♂	17.5		(1)									
	6.4	♀	—			39.2 ± 36.8		(2)	1.6 ± 0.3		(2)	—		
		♂	19.5 ± 1.6		(2)									
saussurei	4.8	♀	29.5		(1)	21.3 ± 28.2		(2)	0.6 ± 0.1		(2)	1.8		(1)
		♂	—											

[1] Female cells are significantly longer than male cells ($t = 2.95$, $df = 15$, $p < 0.05$).

vestibular cell. The 6.4 mm nest contained 3 provisioned cells and 2 vestibular cells. Nest dimensions are shown in Table 2. All cell partitions in the 6.4 mm nest and most partitions in the 9.5 mm nest had a globule of mud at the center of the outer surface. The globules of mud were probably deposited by the female wasps after they detected a chrysidid oviposition hole in a partition. The nests were heavily parasitized by chrysidids.

Prey.—Two cells from the 9.5 mm nest each had 7 spider prey. Identifications of 13 of these spiders are as follows:

ARANEIDAE: 3 ♀♀, 1 ♂ *Araneus pegnia* (Walckenaer); 6 imm. *Eriophora* sp.
THERIDIIDAE: 1 imm. *Argyrodes* sp.
SALTICIDAE: 1 ♀ *Pseudicius* sp.
THOMISIDAE: 1 ♀ *Misumenops* sp.

Life history and natural enemies.—The first 5 cells in the 9.5 mm nest contained developing larvae on January 31. Female *T. lactitarse* emerged on May 23 and 28 from cocoons taken from the first and second cells. A male from the fourth cell emerged on May 22. Male *Neochrysis lecointei* emerged from the third (date undetermined) and fifth cell on March 19. On January 31 the sixth cell contained a first instar chrysidid larva devouring a wasp egg attached to the abdomen of a spider, and the seventh cell con-

tained a chrysidid egg near the inner end and a wasp egg on a spider abdomen near the outer end. Both cell contents were preserved.

The first two cells in the 6.4 mm nest contained wasp cocoons on February 25. Male *T. lactitarse* emerged on May 13 and 14. A chrysidid had presumably emerged from the third cell before the nest was collected, since the cell contained remnants of a chrysidid cocoon.

The cocoon of *T. lactitarse* has been described by Krombein (1956, 1967), Balduf (1961), and Medler (1967) from nests collected in the United States. Cocoons are similar in Costa Rica. The brittle, dark brown cocoons are cylindrical with the posterior end rounded, and the anterior end usually flared outwardly to the walls of the boring, the amount of flare being dependent on the tunnel diameter. Two cocoons from the 9.5 mm nest had the anterior end bluntly rounded. Krombein (1967) reported similar occurrences in large diameter tubes. The anterior face of the cocoon is convex, gray, and more coarsely granular than the rest of the cocoon. In the 9.5 mm nest one cocoon was 15.8 mm long, 5 mm wide at the middle, and 9.0 mm wide at the anterior end. Another cocoon with the anterior end bluntly rounded was 16.4 mm long and 5.2 mm wide.

Trypoxylon (*Trypargilum*) *saussurei* Rohwer

Trypoxylon saussurei, a member of the *spinosum* group of Richards (1934), has been confused with the similar *T. salti* Richards, but the male genitalia are quite different. *T. saussurei* is found in Central America and southern Mexico.

This species occupied a 4.8 mm trap-nest at the cabin porch site at La Pacifica. The nest was indirectly determined to be that of *T. saussurei,* since no adults were reared. Nevertheless, I was able to identify 1 female that died shortly before emerging from the pupa as either *T. salti* Richards or *T. saussurei.* Since numerous males that I have seen from Guanacaste Province have all been *T. saussurei,* I assume that the female is also of that species.

Adult behavior.—On February 7 two wasps slowly flew and hovered around the cabin door. One of them, presumably the female, was examining dark knots and beetle holes and entered a 4.8 mm trap-nest that I held up to her. The nest was attached to the arm of a chair, and the wasp completed it on February 16.

When the female returned to the nest with spider prey, the male left the boring and mounted the female's back as she entered head first. On February 12 and 13 a marked *T. tenoctitlan* female harassed the wasps and once succeeded in entering the nest and chasing the male out. The marked female was forcibly removed with a pair of forceps. The male reentered shortly, followed by the resident female who returned with a spider.

Nest architecture.—The nest contained a preliminary plug at the inner

end of the tube followed by 3 provisioned cells and 2 vestibular cells. The closing plug consisted of a single mass of mud. Nest dimensions are shown in Table 2.

Prey.—The second and third cells contained 12 and 17 spider prey, respectively. Identifications of 28 spiders are as follows:

ARANEIDAE: 1 imm. *Acanthepeira* sp.; 2 imm., 1 ♂ *Araneus pegnia* (Walckenaer); 2 imm. *Larinia directa* (Hentz); 1 imm., 1 ♂ *Metepeira* sp.; 1 imm., 1 ♂ undetermined Araneidae.
PHOLCIDAE: 7 imm. *Physocyclus globosus* (Taczanowski).
OXYOPIDAE: 1 imm. *Oxyopes* sp.
SALTICIDAE: 1 imm. *Bryantella* sp.; 1 imm., 1 ♀ *Corythalia* sp.; 2 ♂♂ *Hentzia* sp.; 2 imm. *Lyssomanes* sp.; 1 ♂ *Rudra* sp.; 1 imm. *Thiodina sylvana* (Hentz).
THOMISIDAE: 1 imm. *Imarus* sp.

Life history.—An egg attached to the side of the abdomen of a pholcid spider was in the third cell. The cocoon is brittle, dark brown and varnished in appearance. It is cylindrical with the posterior end rounded and with a gray collar extending beyond the anterior end.

Discussion

Richards (1934) divided *Trypargilum* into five species groups: *superbum, albitarse, punctulatum, nitidum,* and *spinosum* groups. He also recognized several species complexes within the *nitidum* group: *aureovestitum, excavatum, fugax, nitidum,* and *vagum* complexes. This discussion pertains to the *punctulatum, nitidum,* and *spinosum* groups.

In the *spinosum* group, besides *T. saussurei,* prey and cocoons are known of *T. clavatum clavatum* Say (Krombein, 1967), *T. clavatum johannis* (Richards) (Krombein, 1967), *T. californicum* (=*arizonense,* Matthews and Matthews, 1968), and *T. texense* (Kurczewski, 1963; Lin, 1969; personal obs. of cocoons). Lin (1969) also reported on prey of another species, *T. spinosum* Cameron. As pointed out by Matthews and Matthews (1968) the prey of the *spinosum* group include a wide variety of spider families with as many wandering spiders (those that pursue or ambush prey, e.g., Oxyopidae, Salticidae, and Thomisidae), as snarebuilders (those that entangle their prey in webs, e.g., Araneidae, Pholcidae, and Theridiidae). The general pattern of prey preferences in *Trypargilum* are often still evident when sample sizes are small, as in *T. saussurei* (N = 28). Cocoons of all *spinosum* group species have a gray collar that extends beyond the anterior end (Fig. 6).

Within the *nitidum* group biological data exist only for representatives of the *nitidum* complex, *fugax* complex, and a species of uncertain placement, *T. tridentatum* Packard (Krombein, 1967). In the *nitidum* complex, besides

T. nitidum schulthessi, prey and cocoons are also known of *T. collinum collinum* Smith (Krombein, 1967), *T. collinum rubrocinctum* (Packard) (Krombein, 1967), and *T. orizabense* Richards (Coville, 1979). Their prey include primarily snarebuilding spiders, and their cocoons have a truncate anterior end that bears a small median nipple (Figs. 1 and 3). Cocoons of *T. nitidum schulthessi* and *T. collinum* are virtually indistinguishable (Fig. 1), but those of *T. orizabense* are relatively more elongate (Fig. 3). Prey of *T. tridentatum* are similar to the *nitidum* complex. However, cocoons of *T. tridentatum* have a more rounded anterior end, and often have a weak nipple (Fig. 2).

Cocoons of *T. tenoctitlan* Richards (*nitidum* group, *fugax* complex, Figs. 4 and 5) described by Coville and Coville (1980) are indistinguishable from those of *T. lactitarse* (*punctulatum* group). Cocoons of both species have the anterior end flaring outwardly to the walls of the nesting tube. This suggests that the *punctulatum* group and the *fugax* complex are closely related. In fact, Bohart and Menke (1976) have suggested combining the *punctulatum, nitidum,* and *spinosum* groups on the basis of adult morphology. Cocoon characteristics of the *punctulatum* and *spinosum* groups are no more distinctive than those of species complexes of the *nitidum* group.

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